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SOUTHERN PINE BEETLE-INDUCED MORTALITY OF PINES WITH NATURAL AND ARTIFICIAL RED-COCKADED WOODPECKER CAVITIES IN TEXAS

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ABSTRACT.—Southern pine beetle (*Dendroctonus frontalis*) infestation is the major cause of mortality for Red-cockaded Woodpecker (*Picoides borealis*) cavity trees in loblolly (*Pinus taeda*) and shortleaf (*P. echinata*) pines. Recent intensive management for Red-cockaded Woodpeckers includes the use of artificial cavity inserts. Between 1991 and 1996 we examined southern pine beetle infestation rates of pines with natural vs artificial cavities in loblolly and shortleaf pine habitat on the northern portion of the Angelina National Forest. No significant difference existed in the rate at which southern pine beetles infested and killed pines with natural cavities vs those with artificial cavity inserts ($\chi^2 = 0.84$, $P > 0.05$). Southern pine beetles infested and killed 20 natural cavity trees (25.6%) during the 5-year study (78 cavity-tree years) and 19 artificial cavity trees (18.8%; 101 cavity-tree years). Data for the entire Angelina National Forest indicate that 40% (25 of 62) of the cavity trees killed by southern pine beetles between 1984 and 1996 had been the nest tree during the preceding breeding season. The annual infestation rate of cavity trees appears to be related to southern pine beetle population levels of the surrounding forest. Use of artificial cavities is essential to maintain sufficient numbers of usable cavities for Red-cockaded Woodpeckers in Texas. Why southern pine beetles appear to preferentially infest active Red-cockaded Woodpecker cavity trees is still unknown, but may be related to southern pine beetle attraction to resin volatiles produced when woodpeckers excavate resin wells and/or changes in the levels of infestation-inhibiting tree volatiles as a result of cavity and resin well excavation. *Received 8 April 1997, accepted 23 Sept. 1997.*

Cavity trees are a critical resource for Red-cockaded Woodpeckers (*Picoides borealis*) (Ligon 1970; Lennartz et al. 1987; Walters et al. 1988, 1992). They are essential for reproduction and roosting, require a long period of time to excavate (Conner and Rudolph 1995a), and are often limited in availability (Conner and Rudolph 1989, Costa and Escano 1989, Walters et al. 1992). During the past decade, several studies attributed severe Red-cockaded Woodpecker population declines to several factors, among which was limited availability of cavity trees (Conner and Rudolph 1989, Costa and Escano 1989). Cavity tree mortality, which may further reduce cavity tree availability, may be of great importance for management and recovery of Red-cockaded Woodpecker populations.

The development and use of artificial Red-cockaded Woodpecker cavities to reduce shortages of cavities and facilitate population expansion through the formation of new woodpecker groups has greatly enhanced the forest manager's ability to recover dwindling populations (Copeyon 1990, Copeyon et al. 1991, Allen 1991). Use of artificial cavities has contributed to Red-cockaded Woodpecker population increases in Texas (Conner et al. 1995), Mississippi (Richardson and Stockie 1995), North Carolina and Georgia (Carter et al. 1995), and South Carolina (Gaines et al. 1995, Watson et al. 1995).

The major cause of Red-cockaded Woodpecker cavity tree mortality in loblolly (*Pinus taeda*) and shortleaf (*P. echinata*) pines is pine bark beetle infestation (Conner et al. 1991, Ross et al. 1995). Of 26 Red-cockaded Woodpecker populations on U.S. Forest Service lands, 19 are primarily associated with loblolly or shortleaf pine habitat (Costa and Escano 1989). Thus, pine bark beetle-induced mortality of cavity trees is a significant potential problem throughout the range of the woodpecker. The majority of bark beetle infestations are primarily composed of southern pine beetles (*Dendroctonus frontalis*). Four other pine bark beetles often occur in association with southern pine beetle infestation in

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varying proportions. These include three species of engraver beetles (*Ips avulsus, I. grandicollis,* and *I. calligraphus*) and, occasionally, black turpentine beetles (*Dendroctonus terebrans*). In this paper, we focus on cavity-tree mortality induced primarily by southern pine beetles.

In Texas, artificial cavities, primarily cavity inserts, have been used regularly to provide sufficient cavities for woodpecker groups that have lost active cavity trees to southern pine beetle infestation (Conner et al. 1995, Rudolph and Conner 1995). However, when Red-cockaded Woodpeckers begin to use artificial cavity inserts and peck resin wells, southern pine beetles infest and kill pines containing cavity inserts, apparently finding them as attractive for infestation as natural cavity trees (Conner and Rudolph 1995b).

We compared the beetle infestation rates of pines containing natural Red-cockaded Woodpecker cavities with pines containing artificial cavities over a 5-year period on the Angelina National Forest. We evaluated instances where only a single Red-cockaded Woodpecker cavity tree was infested and killed. Cavity trees can also be infested and killed as the result of the "growth" of an expanding beetle spot (multiple tree infestation; Billings and Varner 1985, Conner et al. 1995b); no cavity tree deaths resulting from beetle spot growth were observed on the Angelina National Forest during our study.

Red-cockaded Woodpeckers create a resin barrier on the pine's bole that serves as a barrier against rat snakes (*Elaphe* spp.; Jackson 1974, Rudolph et al. 1990). The resin system of pine trees serves as their primary defense against southern pine beetles and some pines with superior resin output can survive beetle attack (Lorio 1986). Pines that are able to produce more resin might be preferentially selected by woodpeckers because they would provide better resin barriers against rat snakes and potentially be more resistant to southern pine beetle infestation. Nebeker and coworkers (1992) observed that wound-induced resin flow rate, total resin flow, and viscosity in loblolly pines were genetically controlled. Red-cockaded Woodpeckers may be able to detect the ability of a pine to produce resin when they begin to excavate a cavity start. In contrast, a cavity tree is selected for a cavity insert based on the openness of its bole and a sufficient diameter (38 cm) at the height of installation to physically contain the cavity insert. No consideration is made for the potential resin production of the trees. This suggests that pines with cavity inserts may be more susceptible to mortality following southern pine beetle infestation, since on the average, they might produce less resin than trees selected by woodpeckers. We hypothesized that pines selected by biologists for installation of cavity inserts were more likely to be infested by southern pine beetles than pines selected by woodpeckers for natural cavity excavation.

We also compared the number of Red-cockaded Woodpecker cavity trees killed by southern pine beetle infestation per year (only single tree infestations, not cavity-tree mortality resulting from beetle spot growth) with beetle population levels in forest stands surrounding woodpecker cavity-tree clusters, and determined the number of active cavity trees killed each year by bark-beetle infestation relative to the total number available.

STUDY AREA AND METHODS

We studied southern pine beetle infestation of Red-cockaded Woodpecker cavity trees on the Angelina National Forest (62,423 ha; 31° 15′ N, 94° 15′ W) in eastern Texas. The northern portion of the Angelina National Forest is predominantly covered by loblolly and shortleaf pines, whereas longleaf pine (*Pinus palustris*) is the dominant tree species on the southern portion of the forest in the areas where Red-cockaded Woodpeckers are found (Conner and Rudolph 1989). The loblolly-shortleaf pine habitat where Red-cockaded Woodpecker clusters occur on the northern portion of the Angelina National Forest is located primarily on mesic, shrink-swell clays (Woodtel and LaCerda soil types), which readily support growth of hardwood vegetation (Fuchs 1980, Conner and Rudolph 1995). Varying moisture conditions throughout the year produce the shrink-swell characteristics of the soils, which can strip root hairs off lateral pine roots, increasing stress and pine susceptibility to southern pine beetle infestation (Lorio et al. 1982, Mitchell et al. 1991, Conner and Rudolph 1995). The longleaf pine habitat where Red-cockaded Woodpeckers occur on the southern portion of the Angelina National Forest is located primarily on deep loamy sands (Tehran and Letney soil types) containing materials of volcanic origin (Neitsch 1982). These soils contain very little organic material resulting in a low water holding capacity. High soil temperatures during summer reduce the water holding capacity in these soils, retarding the growth of hardwoods on these sites and stressing pines, but do not usually affect longleaf pine resin production or increase the susceptibility of these longleaf pines to southern pine beetle infestation. Historically, southern pine beetle infestation of cavity trees in the longleaf pine habitats of the Angelina National Forest has been minimal (Conner et al. 1991).

We made annual spring visits to all Red-cockaded Woodpecker cavity trees on the Angelina National Forest (1983 through 1996) to evaluate cavity tree status and condition using the indicators described by Jackson (1977, 1978). Cavity tree clusters occupied by woodpeckers were visited several times per year. We determined the occurrence and causes of all cavity tree mortality (Conner et al. 1991, Conner and Rudolph 1995). Cavity trees infested by southern pine beetles typically had numerous white "popcorn-like" pitch tubes of crystallized pine resin around wounds on the bole where individual beetles had chewed through the bark and into the cambium. Dead cavity trees with signs of bark beetle infestation were examined to determine whether lightning strike was also associated with tree death or if the infestation was caused by other species of bark beetles. Cavity-tree mortality caused by lightning, wind action, and fire have been reported previously (Conner et al. 1991, Conner and Rudolph 1995c).

As part of intensive efforts to recover Red-cockaded Woodpecker populations, a program of cavity insert installation (Allen 1991) began on the Angelina National Forest during 1990 (see Conner et al. 1995). A total of 399 cavity inserts was installed on the northern and southern portions of the forest between January 1990 and spring 1996: 57 between early 1990 and spring 1991, 50 between summer 1991 and spring 1992, 59 during 1992–1993, 31 during 1993–1994, 139 during 1994–1995, and 63 during 1995–1996. Cavity inserts were installed primarily within active woodpecker clusters, but also within inactive clusters and recruitment stands near active clusters.

We used χ^2 analysis to compare southern pine beetle infestation rates of artificial and natural cavity trees in 11 active woodpecker clusters on the northern portion of the Angelina National Forest over a 5-year period between October 1991 and May 1996. We also used χ^2 analysis to evaluate the effect of recency of natural cavity completion or artificial insert activation on likelihood of beetle infestation, as well as the likelihood of beetle infestation of active cavity trees used for nesting and roosting.

To compare southern pine beetle population levels with annual losses of cavity trees, we obtained records of the annual number of southern pine beetle infestations (beetle spots) and the number of pines infested on the northern portion of the Angelina National Forest from the USDA Forest Service Pest Management Office in Pineville, Louisiana, and Atlanta, Georgia (SPBIS—Southern Pine Beetle Information System data base). Pearson correlations were calculated to examine relationships between annual, beetle-induced cavity-tree mortality in 11 cavity-tree clusters on the northern portion of the Angelina National Forest and yearly measures of southern pine beetle population levels in the surrounding forest stands.

RESULTS

Southern pine beetle infestation of Red-cockaded Woodpecker cavity trees has occurred regularly in loblolly and shortleaf pines on the Angelina National Forest over the past 14 years, killing 2–40% of the active cavity trees annually (Fig. 1). Bark beetle-induced mortality of active cavity trees increased after the intensity of woodpecker management increased in the early 1990s following the detection of severe population declines and litigation (Conner and Rudolph 1995b, Conner et al. 1995). Since 1983 on the entire Angelina National Forest, 25 of 62 southern pine beetle-killed cavity trees (40%) had been nest trees during the preceding breeding season. Over a 14-year period an average of 23.1% of the active cavity trees were nest trees in a given year [376 active cavity-tree years (number of active cavity trees each year summed over the 14 years) vs 87 nest tree years in loblolly and shortleaf pines on the Angelina National Forest]. The 40% infestation rate of nest trees is significantly greater than what would be expected based on the ratio of active cavity trees to nest trees on the average (40% vs 23%, $\chi^2 = 13.85$, $P = 0.001$).

Between 1990 and 1996, 399 cavity inserts were installed on the Angelina National Forest. Eighty-seven of these artificial cavities were installed in the 11 active woodpecker clusters we examined closely in loblolly and shortleaf pines on the northern portion of the forest. As a result of cavity-tree losses to southern pine beetles and cavity enlargement by Pileated Woodpeckers (*Dryocopus pileatus*; Conner et al. 1991), most active cavity trees used by Red-cockaded Woodpeckers since 1991 have contained artificial cavities (Fig. 2). During 1992 52% of active cavity trees contained artificial cavities, 63% in 1993, 49% in 1994, 56% in 1995, and 61% in 1996, averaging 56.4% over a 5-year period.

Southern pine beetles infested and killed 39 natural and artificial cavity trees in loblolly and shortleaf pines in the 11 active clusters examined between 1991 and 1996. Of the 39 cavity trees killed by beetles between the fall of 1991 and the summer of 1996, 32 were active and 7 were inactive. Eleven of the 32

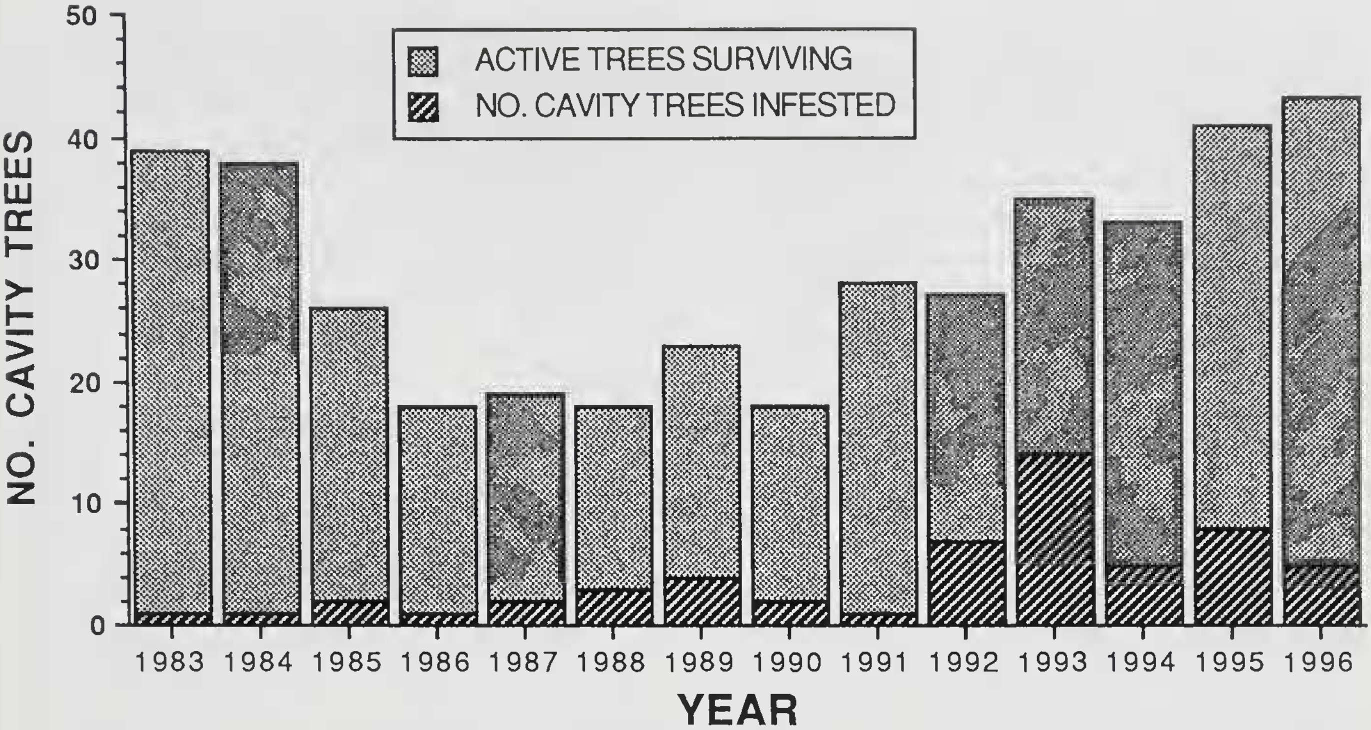


FIG. 1. Number of active Red-cockaded Woodpecker cavity trees and the number of cavity trees infested and killed by southern pine beetles on the northern portion of the Angelina National Forest from 1983 through 1996.

active cavity trees (34%) had been nest trees during the preceding breeding season, 15 (47%) had been roost trees for several years, and in 6 (19%) cavity trees, cavities had been completed just prior to infestation. Relative to their availability, nest trees on the northern portion of the Angelina National Forest were infested at a higher rate than active cavity trees used only for roosting (χ^2 = 4.6, P = 0.032).

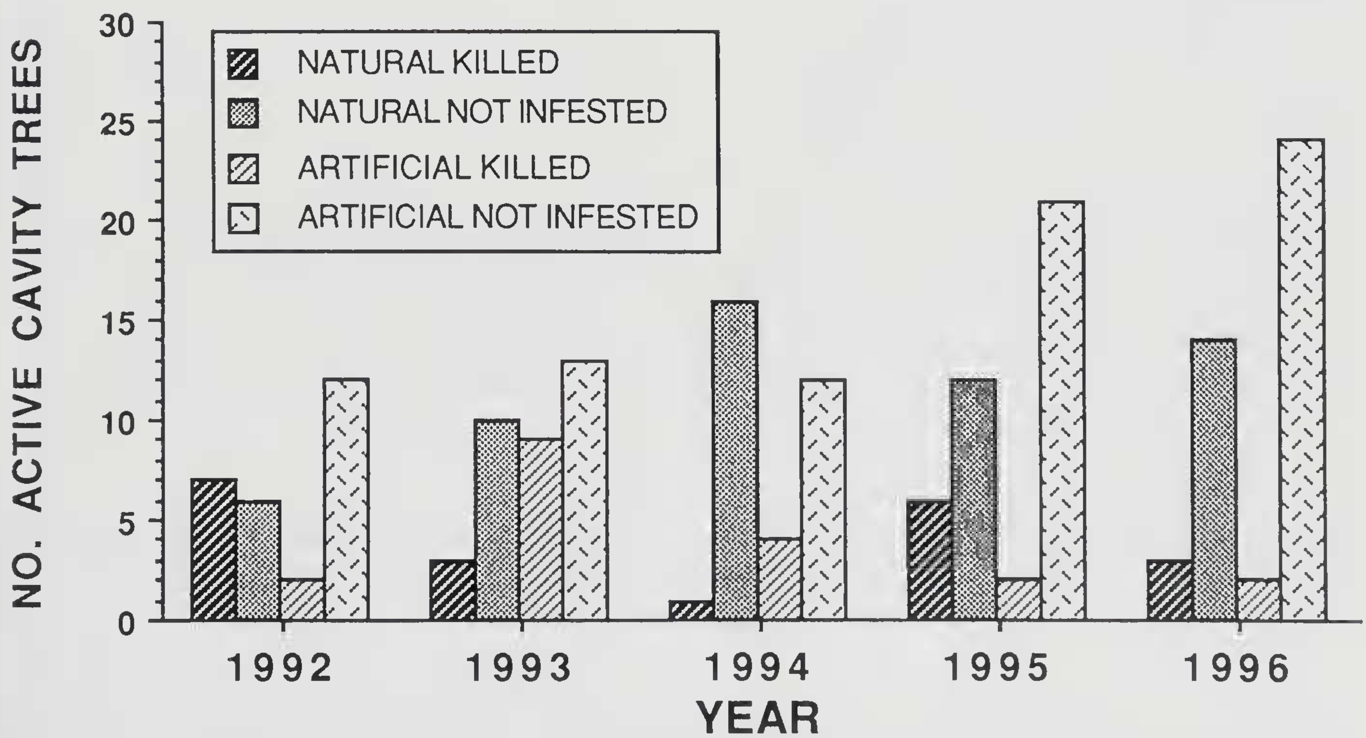


FIG. 2. The number of active Red-cockaded Woodpecker cavity trees with artificial and natural cavities in loblolly and shortleaf pines compared to the number infested and killed by southern pine beetles in eleven cavity-tree clusters on the northern portion of the Angelina National Forest between 1992 and 1996.

During the 5-year study, 20 (25.6%) natural cavity trees (78 cavity-tree years) were killed by southern pine beetles whereas 19 (18.8%) artificial cavity trees (101 cavity-tree years) were killed. Pines with natural cavities and pines with artificial cavities did not differ in the rate at which they were infested by southern pine beetles (Fig. 2; 25.6% vs 18.8%, $\chi^2 = 0.84$, adjusted for continuity, $P > 0.05$).

The recency of natural cavity completion and occupation of artificial inserts by woodpeckers, both of which included the excavation of a series of resin wells around the cavity entrances, affected the likelihood of bark beetle infestation. Over the 5-year period between 1992 and 1996, 24.5% of active cavity trees (24 of 98) were infested and killed within one year of natural cavity completion or use of cavity inserts, whereas only 7.9% of active cavity trees (13 of 164 cavity-tree years) were killed after the first year of their completion or use, respectively ($\chi^2 = 13.9$, $P = 0.001$).

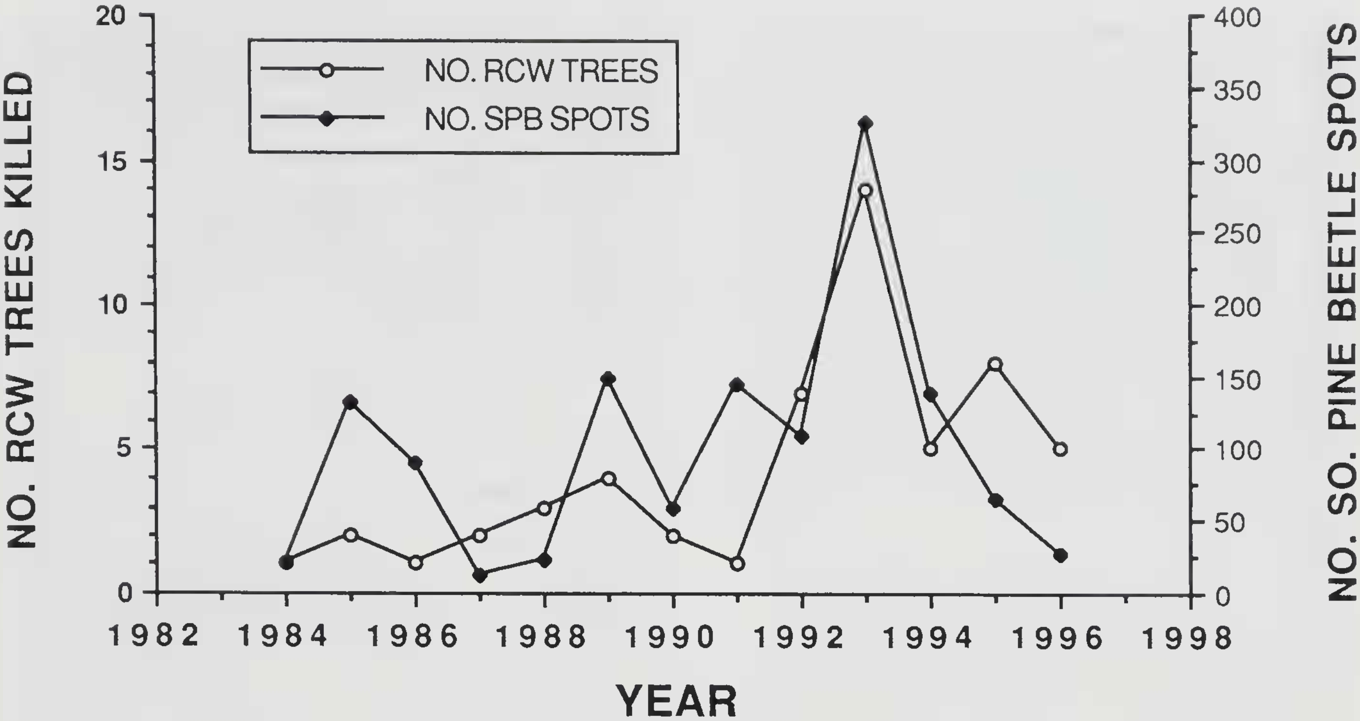
Cavity-tree mortality occurring in pines with artificial cavity inserts (31.1%) during the first year of occupation was not significantly greater than mortality in newly completed natural cavity trees (18.9%; $\chi^2 = 1.97$, $P > 0.05$). However, during the four years following insert occupation or natural cavity completion, only 1.39% of the cavity trees with artificial inserts (1 of 72 cavity-tree years) were killed by bark beetles compared to 13.04% of natural cavity trees (12 of 92 cavity-tree years; $\chi^2 = 7.52$, $P = 0.006$). This suggests that active cavity trees with inserts that survive their first year have a high probability of surviving at least four more years.

Southern pine beetle-induced mortality of Red-cockaded Woodpecker cavity trees on the northern portion of the Angelina National Forest was positively correlated with outbreaks of southern pine beetles in the surrounding forest stands (Fig. 3). Cavity tree mortality was correlated with both the number of southern pine beetle spots ($r = 0.667$, $P = 0.013$) and the number of pines infested ($r = 0.673$, $P = 0.012$) in forest stands surrounding woodpecker cluster areas.

DISCUSSION

Southern pine beetle-induced mortality of Red-cockaded Woodpecker cavity trees in loblolly and shortleaf pine habitat on the Angelina National Forest and many other forests in the South has a substantial impact on the availability of woodpecker cavity trees (Conner and Rudolph 1995, Rudolph and Conner 1995). Between 1983 and 1988 the infestation of single Red-cockaded Woodpecker cavity trees by southern pine beetles averaged about 1.7 cavity trees per year on the Angelina National Forest. Subsequent to intensification of management activities during the late 1980s to halt severe woodpecker population declines, the mean number of single cavity trees infested and killed by southern pine beetles increased significantly, more than tripling that observed previously (5.7/y; see Conner and Rudolph 1995b). As suspected by Conner and Rudolph (1995b), cavity tree infestation rates are significantly correlated with outbreaks of southern pine beetles in surrounding forest stands. However, the apparent preference of southern pine beetles for active as opposed to inactive cavity trees is still not fully understood (Conner and Rudolph 1995b, Rudolph and Conner 1995). Because of these substantial cavity-tree losses to bark beetles and the extensive use of artificial cavities by Red-cockaded Woodpeckers, most cavity trees currently used by the woodpeckers on the northern portion of the Angelina National Forest contain artificial cavities. Fortunately, Red-cockaded Woodpeckers roosted and nested readily in artificial cavities relative to natural cavities during our study and other previous studies (Copeyon 1990, Allen 1991). The importance of this management technique for Red-cockaded Woodpecker recovery in areas where bark beetles are abundant is obvious.

Our hypothesis that pines with artificial cavity inserts would be more susceptible to southern pine beetle infestation than natural cavity trees was incorrect. Artificial cavity trees were not infested and killed by southern pine beetles more or less often than natural cavity trees. This suggests that characteristics used by forest biologists on the Angelina National Forest to select pines for cavity insert installation (open boles and at least 38 cm diameter at 6 m above the ground) may not have been substantially different from those used by Red-cockaded Woodpeckers during their selection of natural cavity trees. Clearly, forest management is not creating a biological sink for Red-cockaded Woodpeckers by installing cavity inserts to re-



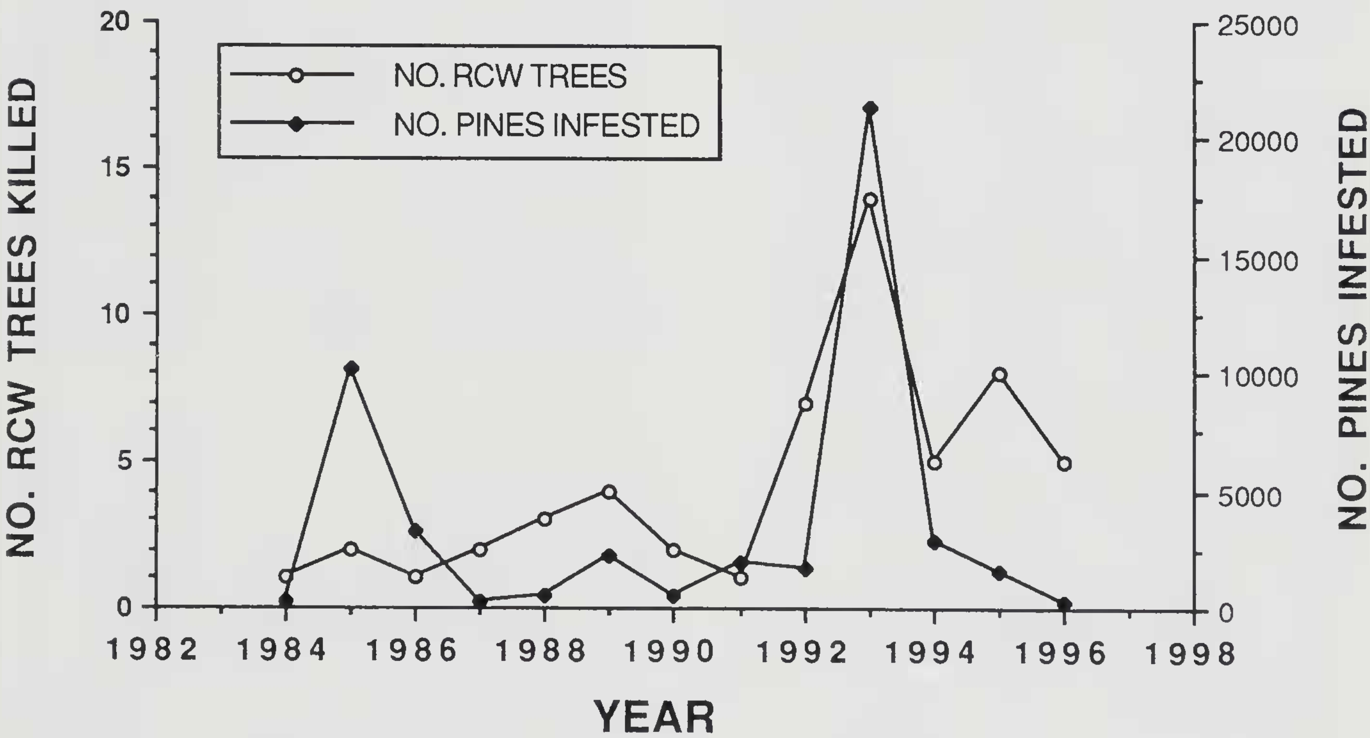


FIG. 3. The number of single Red-cockaded Woodpecker cavity trees that were infested and killed by southern pine beetles (SPB) versus the number of beetle infestations (top) and the number of pines infested by beetles (bottom) on the northern portion of the Angelina National Forest from 1983 through 1996.

place lost natural cavity trees and provide sites for woodpecker population expansion. In fact, loblolly and shortleaf pines chosen by biologists to be artificial insert trees that survived the first year of use by Red-cockaded Woodpeckers had a lower probability of being infested by bark beetles than occupied natural cavity trees. The reason for the lower infestation rate of occupied, insert cavity trees after the first year remains unknown.

Newly completed natural cavities and recently activated artificial cavities were infested at a greater frequency than cavity trees that had been active for more than one year. This was particularly true for trees with cavity inserts, suggesting that effective use of southern pine beetle repellents such as the pheromone verbenone (Payne and Billings 1989, Billings and Upton 1993) and the host tree volatile phenylpropanoid 4-allylanisole (Strom et al. 1995, Hayes et al. 1996) during the first year of insert use by Red-cockaded Woodpeckers may substantially reduce bark beetle-induced mortality to cavity trees containing artificial inserts.

There are several possible reasons why recently activated insert trees had a higher mortality rate than newly completed natural cavity trees. Excavation of natural cavities can take an extended period of time, often as much as 2 to 6 years (Conner and Rudolph 1995a). During cavity excavation and the gradual inclusion of resin wells around the cavity entrance the pine tree may have time to respond to the wounding by adding radial traumatic resin ducts and increasing resin production (Gerry 1922, Hodges et al. 1979, Nebeker et al. 1988, Ross et al. 1997). When installed cavity inserts are used by Red-cockaded Woodpeckers, the process of installation and resin well excavation often occurs in a fairly short period of time (less than a week to several months). Resin produced over a short period of time following an initial wounding is thought to be preformed resin (Nebeker et al. 1988) and not elevated production resulting from a wounding response (Gerry 1922, Harper and Wyman 1936). This sudden wounding of pines with cavity inserts followed by immediate use and resin well excavation by Red-cockaded Woodpeckers may increase their relative susceptibility to bark beetle infestation by reducing the pine's preformed resin. Excessive wounding of pines during turpentining for naval stores weakened pines and occasionally precipitated attack by bark beetles (Wyman 1932).

A significantly higher percentage of cavity trees (artificial and natural) killed by southern pine beetles had been nest trees within one year of beetle infestation. Cavity trees used for nesting are probably the most important trees for woodpecker groups and typically have numerous resin wells that produce copious amounts of fresh pine resin (R. Conner, C. Rudolph, and D. Saenz, pers. obs.). Previous research has demonstrated that active cavity trees are killed at a higher rate than inactive cavity trees (Conner and Rudolph 1995b, Rudolph and Conner 1995). The amount of resin produced by loblolly and shortleaf pines is highly variable depending in part on tree growth form, soil factors, moisture, and season of year (Schopmeyer and Larson 1955; Lorio 1986; Ross et al. 1993, 1995). The apparent attractiveness of active cavity trees with copious resin flow to southern pine beetles suggests that some component of resin volatiles, the amount of resin volatiles produced, or stress exerted on the pines by extensive resin well excavation may increase the preference/vulnerability of such cavity trees to southern pine beetle attack.

Southern pine beetles are attracted to and aggregate on pines where the resin volatile alpha-pinene (a major component of pine resin) and the beetle pheromone frontalin are present. The combination of these two chemicals serves as a strong attractant for southern pine beetles (Thatcher et al. 1980). Alpha-pinene, alone, does not appear to serve as a primary attractant to southern pine beetles (Thatcher et al. 1980, Billings 1985). Thus, it is somewhat perplexing why southern pine beetles are attracted to active loblolly and shortleaf pine cavity trees at a higher rate than to inactive cavity trees.

Site disturbance (Coulson et al. 1986, Flamm et al. 1993) and lightning strikes (Coulson et al. 1983, Lovelady et al. 1991) have been shown to be associated with the infestation of pines by southern pine beetles. Such disturbances apparently increase the attractiveness of pines for an initial attack by southern pine beetles. Woodpecker excavation of resin wells on cavity trees may sufficiently stress loblolly and shortleaf pines that they take on characteristics of pines suffering other types of stress.

The mechanism by which southern pine beetles select Red-cockaded Woodpecker cavity trees for initial attack may relate in part to the pine's production of allylanisole. This host volatile, produced by healthy pines, is known to inhibit infestation by southern pine beetles and other bark beetles (Hayes and Strom

1994, Hayes et al. 1994). Reduced levels of allylanisole have been associated with southern pine beetle attack and successful infestation of pines. Research is needed to evaluate the relative contributions of allylanisole reduction and alpha-pinene elevation resulting from Red-cockaded Woodpecker activity at resin wells toward increasing the attractiveness of pines to southern pine beetles.

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